

Adjusting to a toxic invader: native Australian frogs learn not to prey on cane toads

Matthew J. Greenlees, Benjamin L. Phillips, and Richard Shine

School of Biological Sciences A08, University of Sydney, New South Wales 2006, Australia

Biological invasions provide opportunities to study novel behavioral interactions between predators and their prey. To withstand detrimental effects from a potentially lethal invader, a native taxon must somehow adjust to the invader's presence. Cane toads (*Bufo marinus*) are highly toxic to native Australian anurans and constitute a major threat if consumed. We recorded the responses of Australian marbled frogs (*Limnodynastes convexusculus*) during their first encounters with edible-sized cane toads. The frogs exhibited rapid avoidance learning: toad-exposed frogs were less likely to attack subsequently encountered cane toads (and hence more likely to survive). Among-clutch variance in learning rates and in physiological tolerance to toad toxins was low, suggesting that genetically based adaptive changes to frog feeding responses will be slow (especially given that rapid learning reduces mortality and thus reduces the fitness decrement of initial willingness to attack a toad). Hence, rapid taste aversion learning is the primary mechanism enabling marbled frogs to persist in the presence of a potentially fatal invader. In combination with previous work, our study shows that some native predators adjust to the threat posed by cane toad invasion via taste aversion learning, whereas others show genetically based modification of feeding responses. More generally, both learning and adaptation enable vulnerable native taxa to survive the arrival of a toxic invasive species. *Key words*: behavior, *Bufo marinus*, frog, invasive species, learning, predator. [*Behav Ecol* 21:966–971 (2010)]

The arrival of an invasive species generates novel challenges for local taxa. That fact was first recognized over 50 years ago (Elton 1958), but a recent resurgence of research on the topic has clarified the ways in which invaders can influence local species via ecological interactions such as predation (Dickman 1996; Roemer et al. 2002; Salo et al. 2007) and competition (Blanchet et al. 2007; Bohn et al. 2008; Orrock et al. 2008). The ability of native taxa to adjust to the presence of invasive species has implications not only for the short-term impacts of the invader on individual species but also for longer term impacts on species assemblages and the interactions within them (Carroll 2007). Due to its geographic isolation, Australia lacks representatives of many phylogenetic lineages that are common throughout much of the rest of the world. That isolation has rendered Australia especially vulnerable to biotic invasions (Dickman 1996; Low 1999; Banks et al. 2000). One such phylogenetically novel invasive species in Australia is the cane toad (*Bufo marinus*; allocated to *Chaunus* or *Rhinella* by some authorities: Frost et al. 2006), notable for the breadth and severity of its impact on native fauna (Boland 2004; Doody et al. 2006; Greenlees et al. 2006, 2007; Griffiths and McKay 2007).

Cane toads are large anurans, endemic to South America, and have been deliberately introduced to many countries for biological control of insect pests (Mungomery 1936; Lever 2001). Cane toads have since spread widely and are listed as one of the world's 100 worst invasive species (International Union for Conservation of Nature 2008). The potent toxin of these large anurans is fatal to many predators (reptiles and mammals) in the introduced range that lack coevolved physiological or behavioral adaptations to deal with the toads (Covacevich and Archer 1975; Burnett 1997; Phillips and

Fitzgerald 2004; Smith and Phillips 2006; Letnic et al. 2008). In the face of toad invasion, such native predators may be under strong pressure not to consume this toxic anuran. Australian blacksnakes (*Pseudechis porphyriacus*) exhibit rapid adaptive shifts in feeding responses, gape-limiting feeding structures, and toxin resistance that reduce their vulnerability and hence facilitate coexistence with cane toads (Phillips and Shine 2006b). Laboratory trials on this species suggest little or no ability to learn to avoid toads as prey, despite repeated exposure (Phillips and Shine 2006b). In contrast, some other potentially vulnerable predator species (fishes: Crossland 2001; marsupials: Webb et al. 2008) demonstrate rapid aversion learning, enabling coexistence with cane toads via changes to phenotypically plastic feeding responses. The relative importance of adaptation versus aversion learning in enabling other Australian predators to deal with the toxic toads remains unknown.

One group of Australian predators of particular interest in this respect is the Anura. Frogs are diverse and abundant in many Australian habitats, and the broad morphological, physiological, and ecological similarities of many species to the introduced toad means that encounter rates between native and invasive anurans likely will be high. Experimental studies suggest that competition for prey between toads and frogs is unlikely to be important (Greenlees et al. 2006), nor is predation by toads on frogs (cane toads rarely consume vertebrate prey: Zug and Zug 1979; Freeland 1984; Lever 2001). However, direct poisoning of native frogs due to toad ingestion may be important, as it is for other vertebrate predators (squamates, crocodylians, and marsupials: Burnett 1997; Smith and Phillips 2006; Webb et al. 2008).

What life-history stage of native anurans is likely to be most vulnerable to toad-induced poisoning? The larvae of native anurans are very sensitive to toad toxins (Alford et al. 1995; Crossland and Alford 1998; Crossland 2000) and die in large numbers when they attempt to eat the eggs of cane toads in natural waterbodies (Crossland et al. 2008). Another plausible interaction—the possibility of predation by postmetamorphic

Address correspondence to M.J. Greenlees. E-mail: greenlees.matt@gmail.com.

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frogs on small toads—remains unstudied. Many Australian frogs are anurophagous (Barker et al. 1995; Pyke and White 2001), and cane toads metamorphose at very small (and hence edible) body sizes (Lever 2001). Given that recently metamorphosed frogs and toads will both be concentrated around waterbodies, toads may imperil postmetamorphic native anurans that attempt to ingest these toxic newcomers. Does this happen? And if so, do native frogs respond by rapid learning, as has been reported in fish (Crossland 2001) and planigales (Webb et al. 2008), or by genetically based adaptive shifts (as in blacksnakes of Phillips and Shine 2004, 2006b)? We conducted experimental trials to answer these questions.

MATERIALS AND METHODS

Study animal

Marbled frogs (*Limnodynastes convexiusculus*) are terrestrial Limnodynastids (formerly Myobatrachids; see Frost et al. 2006) growing to 55 mm snout–urostyle length. They inhabit savannah woodlands, lowland scrubs, and floodplains in coastal and near coastal areas of northern Australia (Cogger 1999). The cane toad invasion has encompassed approximately 80% of the range of marbled frogs and ultimately is likely to occupy the entire range of this native species (Urban et al. 2007). Marbled frogs prey primarily on insects (Tyler and Cappel 1983), but our field and laboratory observations reveal that these frogs also feed readily on other anurans.

Collection and husbandry

Experiment 1: comparing behavior and vulnerability of toad-exposed versus toad-naïve frogs

We studied interactions between marbled frogs and cane toads in the Australian wet–dry tropics 60 km east of Darwin (Northern Territory: 131°18′48.19″E, 12°34′14.81″S). The climate is hot year-round (mean monthly maxima >30 °C in all months), but >75% of the 1400 mm annual rainfall occurs in the monsoonal wet season (December–March), based on readings taken from Middle Point, <5 km from the study site (Australian Government Bureau of Meteorology 2009). Most breeding by native anurans in this area occurs during the wet season (Tyler et al. 1983). At the time the study was conducted, toads had been present at the site for approximately 3 years.

We collected 20 egg clutches of marbled frogs from a temporary pond on the Fogg Dam road on 27 February 2007, the morning after they were all deposited. Although little is known of the breeding biology of marbled frogs, it is likely that different females produced each clutch. The clutches were taken to a research facility <5 km from the collection site, and all clutches hatched within 3 days. Eggs and tadpoles were kept outdoors, initially in plastic containers (38 cm long × 26 cm wide × 20 cm high) in the shade. Eggs and tadpoles from each clutch were kept separately. Tadpoles were reared on a diet of thawed lettuce provided ad libitum. Water was partially changed twice weekly. On 2 May (64 days after laying), 30 tadpoles were randomly collected from each clutch and transferred to mesh baskets (90 cm long × 50 cm wide × 55 cm high) placed in pairs in outdoor plastic containers (105 cm × 105 cm × 65 cm) filled with filtered water. These containers were covered with mesh lids to exclude predators. Algae growing naturally on the mesh baskets provided food for the tadpoles, and thawed lettuce was also provided ad libitum. Water was partially changed at 2-monthly intervals, although rainwater frequently replenished the water through the mesh lids.

Tadpoles were checked for developmental progress (Gosner 1960) once a day after the first tadpole reached Gosner stage

37 (i.e., toes on the hindlimbs fully formed). When tadpoles reached Gosner stage 42 (forelimbs had appeared), they were removed from the outdoor enclosures and housed individually in smaller plastic containers (17 cm long × 12 cm wide × 7 cm high; half water and half land) in a shaded area until metamorphosis.

Experiment 2: comparing initial versus subsequent responses of frogs to toads

We collected adult marbled frogs from Keep River National Park (129°02′21.28″E, 15°58′15.97″S), also in the Northern Territory, in December of 2008, prior to the arrival of toads at that site. Keep River National Park exhibits seasonal patterns of temperature and rainfall similar to those at Fogg Dam and contains similar faunal assemblages. Frogs were transported back to our laboratory at Middle Point and were housed in groups of 3 or 4. Three clutches of eggs were produced and transferred into plastic containers (38 cm long × 26 cm wide × 20 cm high). After 30 days, 60 individuals from each of the 3 clutches were randomly selected and transferred, in groups of 30, into mesh baskets (90 cm long × 50 cm wide × 55 cm high) placed in pairs in outdoor plastic containers (105 cm × 105 cm × 65 cm) filled with filtered water. Husbandry of metamorphosing frogs followed the same procedures as for Experiment 1.

Experimental design

Experiment 1: comparing behavior and vulnerability of toad-exposed versus toad-naïve frogs

Feeding trials commenced within 6 days of individuals reaching Gosner stage 46 (metamorphosis complete). Within each clutch, emerging metamorphs were allocated alternately to either the control group (untrained) or the treatment group (trained). The first allocation per clutch was determined by tossing a coin. In the “untrained” group, individuals were offered a single small cricket (*Acheta domesticus*) on 5 consecutive nights. Individuals in the “trained” group were offered a small cricket initially and then alternately metamorph cane toads and small crickets over the following 4 nights. Prey items were introduced between 1700 and 1800 and left overnight. Uneaten or regurgitated prey items were removed between 0900 and 1000 the next morning. On the sixth night, all individuals (from both the groups) were offered a metamorph cane toad weighing 0.1–0.2 g (mean = 0.13 g, standard deviation = 0.03). Responses of all frogs to the metamorph toads offered as prey on the sixth night were video recorded (using the “nightvision” function) for 1 h after the toads’ introduction. One of us (M.J.G.) blind scored all videos for the interaction between the 2 species (i.e., attack vs. ignore) and any mortality of native frogs.

This experiment was designed to mimic conditions in nature (i.e., metamorph frogs either encountered toads or did not encounter them) so that we could predict shifts in frog behavior as a consequence of encountering toads. However, interpretation of the causal basis of any shift in frog behavior was precluded by the significant mortality occurring in the toad-exposed group. This mortality was unexpected when the experiment was designed, but because a significant number of frogs in the toad-exposed group died after consuming toads during “training” sessions (prior to the videotaped trials), any difference between trained and untrained groups in these final trials could be the result of 2 processes, either (a) the expression of developmental plasticity (aversion learning) in the trained group or (b) differential survival within the toad-exposed group, based on propensity to attack a toad (i.e., the survivors will tend to be the animals that are less likely to attack toads). To discriminate between these 2 possibilities, we needed to

quantify responses of the same individual frogs in their first versus subsequent encounters with toads. Our subsequent experiment (below) was designed for this purpose.

Experiment 2: comparing initial versus subsequent responses of frogs to toads

This experiment directly compared the behavior of metamorph frogs in initial encounters with metamorph toads to that in third encounters. Using the same protocol as for the trained group in the first experiment, all individuals were offered a small cricket initially and then alternately metamorph cane toads and small crickets over the following 5 nights. Prey items were introduced between 1700 and 1800 and left overnight. Uneaten or regurgitated prey items were removed between 0900 and 1000 the next morning. Responses of frogs to metamorph toads both on the second night (first encounter with toads) and the sixth night (third encounter with toads) were video recorded and scored as above.

Statistical analysis

Experiment 1: comparing behavior and vulnerability of toad-exposed versus toad-naïve frogs

To determine whether exposure to toads affected marbled frog behavior and to compare responses among clutches, we used generalized mixed models. Treatment (i.e., trained vs. untrained) was considered as the fixed independent variable and clutch as the random independent variable. For these binomial data (on whether or not a metamorph marbled frog attacked the metamorph toad or whether or not it survived the interaction), we used a binomial error structure and logit link functions. After these analyses, we reran the models, removing clutch as a factor, to compare log-likelihood ratios between models with and without clutch. Improvement in model fit by the addition of clutch was assessed using the likelihood ratio test (Rohlf and Sokal 1995; Hilborn and Mangel 1997).

To investigate potential differences among clutches in behavior or mortality rates, we then pooled the data for each metamorph's first encounter with a cane toad (i.e., the second prey item offered to "trained group" toads and sixth prey item offered to "untrained group" frogs; despite the difference in days since beginning of the experiment, in all cases, these were the specific frog's first encounter with a cane toad). Generalized mixed models were used according to the same protocol above, except that treatment was not incorporated. Initially, we compared feeding responses (i.e., whether or not each frog attacked its toad) among clutches. Then, we restricted the data to frogs that attacked toads and repeated the analysis on mortality rates (i.e., among these toad-attacking individuals, did clutches differ in the relative numbers of survivors vs. deaths?). Improvement in model fit by inclusion of clutch was assessed as above. All models were constructed and analyzed using the lme4 package (Bates 2005) in the R statistical environment (R Core Development Team 2008). As required by the test, the dispersal parameter for the model was close to 1.0 (0.999).

Experiment 2: comparing initial versus subsequent responses of frogs to toads

To determine whether frogs exhibited learned aversion between their first and third encounters with metamorph cane toads, we again constructed a generalized mixed model. The same protocols were used as above to compare differences in whether or not metamorph frogs attacked toads. For this analysis, encounter (either first or third) was incorporated as the fixed independent variable, and because each individual was measured twice, we added an effect of individual within clutch. Again, as only the first encounter was being considered,

data from the 2 treatment groups were pooled. As above, we assessed the effect of clutch in this model using the likelihood ratio test. As required by the model, the dispersal parameter was close to 1.0 (0.999).

Ethical note

All procedures were approved by the University of Sydney Animal Care and Ethics Committee, who judged that any suffering experienced by the animals during the course of these trials was justified by the need to clarify the ecological impacts of invasive cane toads in order to inform conservation and management of the native fauna.

RESULTS

Experiment 1: comparing behavior and vulnerability of toad-exposed versus toad-naïve frogs

A total of 444 individuals survived to the final stage of the experiment (filming of interactions). No individuals from the untrained (control) group died during the experiment (thus, $N = 235$), but 74 individuals from the trained (treatment) group died when they attempted to prey on cane toads (thus, $N = 209$ surviving individuals from the trained group). When tested on the sixth night, individuals from the untrained group were more likely to attack metamorph cane toads ($P < 0.001$; Figure 1a). The consequently higher mortality among untrained frogs ($P = 0.04$; Figure 1b) thus tended to reduce the overall differential in survival rate between the 2 groups by the end of the experiment. The analysis revealed no significant variation among clutches in the proportion of young frogs that attacked (vs. ignored) metamorph toads or in the outcome of those interactions (Table 1).

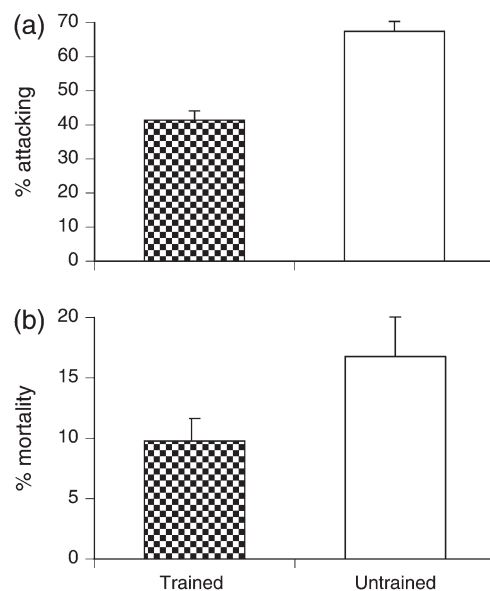


Figure 1
Effect of prior exposure to cane toads (*Bufo marinus*) on behavior and survival probability of marbled frogs, *Limnodynastes convexiusculus*, from 20 clutches of the latter species. The 2 panels compare trained frogs (those with prior exposure to toads) to untrained conspecifics (no prior exposure to toads) in terms of (a) proportion of frogs that attacked cane toads and (b) mortality rates of frogs. Each panel shows mean values per clutch with associated standard error.

Table 1
Results of statistical analyses of interclutch variation in the responses of marbled frogs (*Limnodynastes convexiusculus*) to metamorph cane toads (*Bufo marinus*)

Dependent variable	Error structure	Independent variable	Test statistic	<i>P</i>
Attack or not	Binomial	Treatment (fixed)	$z = 5.26$	<0.001
		Clutch (random)	$\chi^2 = 0$	1
Survived or not	Binomial	Treatment (fixed)	$z = 7.82$	0.04
		Clutch (random)	$\chi^2 = 3.2$	0.074

The table shows the results of analyses of whether or not the frogs interacted (i.e., attacked) the toad and the outcomes of interactions. Significant results are shown in boldface font. Chi-square values were derived from twice the difference between the log-likelihood result with and without the random independent variable (clutch) included in the model.

Examining only the first encounters with metamorph toads, 28 frogs ingested metamorph toads. Eleven of these frogs died and 17 survived. Additionally, 126 individuals attacked and either did not ingest the toad or regurgitated it soon after ingestion. Of these, 64 survived and 62 died. Generalized mixed models indicated no significant variance among clutches in the proportion of individuals willing to attack cane toads ($P = 0.37$; Table 2) or in mortality rates of those that did attack ($P = 0.65$; Table 2).

Experiment 2: comparing initial to subsequent responses of frogs to toads

Twenty-two to 25 metamorph frogs from each of the 3 clutches (total $n = 71$) were filmed in their first encounters with toads. Of those animals, 13–18 per clutch (total $n = 50$) survived to be filmed in their third encounter with a metamorph toad also. Generalized mixed modeling on the mean proportion per clutch attacking in the first versus third encounter showed a significant decrease in attack rate ($z = 4.99$, $P < 0.001$). Fewer individuals attacked toads in the later encounter (Figure 2). These differences clearly indicate learning. Although our sample size for this experiment was low, our model showed no difference between clutches in learning ability ($\chi^2 = 0.20$, $P = 0.89$).

DISCUSSION

Despite widespread speculation about mechanisms and intensities of impact of invasive cane toads on the Australian fauna, robust data are scarce for most potential interactions (Letnic

Table 2
Results of statistical analyses of interclutch variation in the responses of marbled frogs (*Limnodynastes convexiusculus*) to metamorph cane toads (*Bufo marinus*) during their first encounter and the outcome of attacks

Dependent variable	Error structure	Independent variable	Test statistic	<i>P</i>
Attack or not	Binomial	Clutch (random)	$\chi^2 = 0.8$	0.37
Survived or not	Binomial	Clutch (random)	$\chi^2 = 0.2$	0.65

The table shows the results of analyses of the behavior of all frogs toward toads and the outcomes for frogs that did attack toads. Chi-square values were derived from twice the difference between the log-likelihoods with and without clutch included in the model.

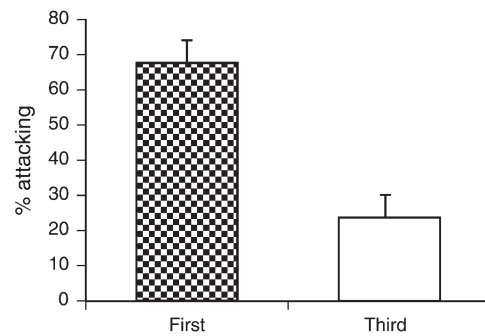


Figure 2
The proportion of marbled frogs, *Limnodynastes convexiusculus*, that attacked cane toads (*Bufo marinus*) in their first versus third encounters with metamorph toads. Mean values per clutch (based on frogs from 3 clutches) are shown with associated standard error.

et al. 2008). Discussions on the impacts of cane toads on native Australian frogs generally have focused on competition (Freeland and Kerin 1988; Catling et al. 1999; Greenlees et al. 2007) or predation by toads (Covacevich and Archer 1975), neither of which seem likely to be as important as fatal poisoning of frogs that attempt to consume toads (Crossland et al. 2008). The small body sizes of native frogs relative to adult cane toads (maximum body masses <100 g vs. >2 kg; Lever 2001; Greenlees MJ, unpublished data) likely is a major reason why the potential impact of poisoning has been neglected. For example, Catling et al. (1999) assumed that only the largest native anuran species would attempt to consume toads and hence be threatened via this mechanism. Our data falsify that assumption. Marbled frogs are small (in our study area, maximum body mass <30 g; mean = 6.06 g), and indeed, the specimens used in our study all weighed <2.1 g. Nonetheless, these frogs readily attempted to consume metamorph cane toads. Almost any anurophagous native anuran species is large enough to prey on the smallest life-history stage of the cane toad (toad metamorphs often are <0.15 g). Similarly, larvae of most local anuran species attempt to consume toad eggs and die in large numbers as a result (Crossland et al. 2008). The clear implication is that lethal toxic ingestion may be a significant mechanism of direct impact of cane toad invasion on Australian frogs.

Both the composition and concentration of toxins possessed by a cane toad change through ontogeny, and toxicity to predators is lowest at the time of metamorphosis (Alford et al. 1995; Longson and Joss 2006; Hayes et al. 2009). Nonetheless, 14% of the marbled frogs that we tested in Experiment 1 (73 of 515) died when they attempted to consume recently metamorphosed toads. Field observations of dead marbled frog metamorphs beside ponds in which toads have recently spawned (Grace and Sawyer 2008; Greenlees MJ, Phillips BL, personal observation) suggest that the same vulnerability is manifested in the field. So, all life-history stages of the cane toad may be toxic enough to imperil at least some species of native predators.

The broad dietary habits of most anurans (Duellman and Trueb 1986) mean that they often encounter prey that is unpalatable: in particular, many invertebrate species possess chemical defense mechanisms (Bowers 1992; Brunet 2000; Eisner et al. 2005). Thus, an ability to rapidly discriminate between palatable and unpalatable prey items may be widespread in anurans (Zavala 1968; Elepfandt 1985; Daneri et al. 2007). Amphibians also can learn to forage in places where food has previously been abundant (Alexander 1964; Waterhouse 1974) and to avoid areas containing the scent

Table 3
Results of statistical analyses of variation in the responses of marbled frogs (*Limnodynastes convexiusculus*) during their first and third encounter with metamorph cane toads (*Bufo marinus*)

Dependent variable	Error structure	Independent variable	Test statistic	<i>P</i>
Attack or not	Binomial	Encounter (fixed) Clutch (random)	$z = -4.99$ $\chi^2 = 0.2$	<0.001 0.89

Chi-square values were derived from twice the difference between the log-likelihood result with and without the random independent variable (clutch) included in the model. Significant results are shown in boldface font.

of predators (Murray et al. 2004). In our experiments, the ability to learn avoidance of cane toads provided a direct fitness benefit (lower mortality: Figure 1b). Toad-experienced frogs were less likely to attack the toxic prey item in subsequent trials (Figures 1a and 2), presumably using either scent or visual cues to discriminate among alternative prey types.

Although the relative contributions of acquired (learning) versus heritable (innate) behavior to the way in which animals forage have been a subject of considerable contention (Richards 1987), the 2 are not mutually exclusive. For example, both processes contribute to optimization of foraging behavior in amphibians (Gibbons et al. 2005). However, our results suggest no significant among-clutch variation in learning ability; all marbled frogs may be capable of learning to avoid toxic prey such as introduced cane toads (Tables 1 and 3). Additionally, our data suggest little variation among clutches in physiological resistance to toad toxins (proportion of predation events that proved fatal to the predator; see Table 2). Hence, marbled frog populations likely adjust to the arrival of the toxic cane toads neither by shifts in the frequency of alternative alleles coding for different foraging responses or physiological resistance to toxins nor by the evolution of learning ability. Instead, marbled frogs rely on phenotypic plasticity in their foraging responses to survive the toad's arrival. More generally, inherent flexibility in behavioral traits may play a critical role in allowing organisms to adjust to unpredictable variation in foraging risks and opportunities (Immelmann 1975; Blanckenhorn and Perner 1994).

A growing body of evidence documents the importance of behavioral modifications in enabling native species to tolerate the presence of invasive species (Hoare et al. 2007; Glenn and Holway 2008). Those behavioral modifications arise partly from phenotypic plasticity and partly from changes in allelic frequencies (Strauss et al. 2006). The accumulating evidence on impacts of cane toads on Australian predators shows that a single invader can elicit both types of responses in different organisms. Morphological, physiological, and behavioral shifts in frog-eating snakes appear to have been driven largely by genetic changes (Phillips and Shine 2004, 2006a, 2006b), whereas phenotypic plasticity may be the most important mechanism by which populations of fishes (Crossland 2000), marsupials (Webb et al. 2008), and anurans (present study) have adjusted to the presence of this invasive species. This diversity may preclude generalizations about the biological processes that mitigate the impacts of an invasive species.

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